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RESOURCE USE BY HERONS IN A YUCATAN WETLAND DURING THE BREEDING SEASON

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ABSTRACT.—During 1986, we studied the habitat, prey type, and prey size used by six species of egrets and herons in the Sian Ka'an Biosphere Reserve (Yucatán, México). The availability of different habitat types, which varies from salt to freshwater and from open to forested wetland, allows the herons to segregate into two groups (1) Great Blue Heron (*Ardea herodias*)—Great Egret (*Casmerodius albus*)—Snowy Egret (*Egretta thula*), that use mainly freshwater habitats, and (2) Reddish Egret (*E. rufescens*)—Tricolored Heron (*E. tricolor*), that use marine habitats. We have no data for Boat-billed Herons (*Cochlearius cochlearius*), because this species is strictly nocturnal, and censuses were conducted at daylight. Prey type and prey size greatly differ among Great Blue Herons, Great Egrets, and Snowy Egrets but overlap considerably between the Reddish Egrets and Boat-billed Herons. We found a positive correlation between size of heron and size of prey, but in our study area prey size is not important in niche segregation, since four of these species eat prey of similar sizes. *Received 7 Jan. 1993, accepted 21 April 1993.*

Many studies of sympatric colonial wading birds in temperate regions have shown that there are differences among species in nest-site placement (Maxwell and Kale 1977; McCrimon 1978; Burger 1978, 1979, 1985; Beaver et al. 1980) and in feeding ecology and behavior (Meyerriecks 1962; Kushlan 1976, 1978; Willard 1977; Custer and Osborn 1978; Whitfield and Blaber 1979; Rodgers 1983; Kent 1986; Fasola 1986). By contrast, studies of wading birds in the Neotropics are rare (Kushlan et al. 1985, Willard 1985, Frederick and Bildstein 1992). In this paper, we present the results of a study of the habitat and prey use by six species of herons, Great Blue Heron (*Ardea herodias*), Great Egret (*Casmerodius albus*), Reddish Egret (*Egretta rufescens*), Tricolored Heron (*E. tricolor*), Snowy Egret (*E. thula*), and Boat-billed Heron (*Cochlearius cochlearius*) during the breeding season in a Neotropical wetland.

STUDY AREA AND METHODS

We studied herons in 1986 at the Sian Ka'an Biosphere Reserve in the Yucatan Peninsula (Quintana Roo, México). The reserve comprises 528,000 ha, including marine habitats such as a coral reef, two large marine bays (180,000 ha), coastal lagoons with associated mangrove forests (totalling 18,000 ha), forests (150,000 ha), freshwater lagoons (20,000 ha), and wetlands (160,000 ha). Wetlands include sawgrass marshes, dominated by common reed (*Phragmites australis*), cattail (*Typha angustifolia*), and specially sawgrass (*Cladium jamaicensis*), and mangrove swamps of small (1.5–2 m tall) red mangroves (*Ryzophora mangle*) (Fig. 1).

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In coastal marshes and swamps, salinity may be high, while inland mangrove swamps and marshes are almost freshwater.

Annual rainfall (1967–1982) ranges from 872 mm to 1436 mm, with an average of 1128 mm, 75% of it falling during the wet season from May to October (López Ornat 1983). During 1986, rainfall was 1059 mm, but monthly distribution did not follow the typical pattern. The wet and dry seasons did not appear well delimited, there was a minimum amount of rain in April and July, and May had the most rain. Mean monthly temperatures varied little during the year, ranging from 22.7°C in January to 27.5°C in May. For a detailed description of study area see López Ornat (1983) and Olmsted et al. (1983).

The nesting period of herons at Sian Ka'an runs from December to June. Great Blue Heron, Reddish Egret, and Boat-billed Heron, are the first to start the breeding cycle, as we found nests with eggs of these species in December. In early March, Tricolored Heron and Great Egret had eggs, and the Snowy Egret began its nesting cycle by mid-March.

During 1986, 36 pairs of Great Blue Herons, 437 pairs of Great Egrets, 168 pairs of Snowy Egrets, 51 pairs of Reddish Egrets, 226 pairs of Tricolored Herons, and 27 pairs of Boat-billed Herons nested on 11 keys in Sian Ka'an (Fig. 1) (López Ornat and Ramo 1992).

Monthly censuses were conducted in different habitats without distance estimates (Verner, 1985) with binoculars (8 × 32). Three transects were covered, two by car and one by boat. The first, 4 km long, located close to the reserve, crossed an area of inland freshwater mangrove swamps (dates, 23 March, 28 April, 29 May, 29 June, and 1 December). The second, 2 km long, ran across sawgrass marshes and coastal saltwater mangrove swamps (dates, 22 March, 27 April, 28 May, 28 June, and 3 December). The last one was surveyed by boat along the Canal de Chunyaxché. It started inland on the freshwater Chunyaxché lagoon, crossed sawgrass marshes and coastal mangrove swamps, and ended at a coastal lagoon, totalling 35 km (dates, 14 March, 20 April, 17 May, 23 June, 2 December). We surveyed 15.5 km of coastal lagoons, 5.5 km of coastal saltwater mangrove swamps, 3 km of sawgrass marshes, 4 km of inland freshwater mangrove swamps, and 13 km of freshwater lagoons. Results are presented as the mean number of wading birds per km for each habitat.

To study diet, we collected regurgitated pellets of six nestlings of Great Blue Herons, 24 of Great Egrets, 14 of Reddish Egrets, 20 of Tricolored Herons, 15 of Snowy Egrets, and five of Boat-billed Herons. Pellets were preserved in 10% formalin and later were transferred to 70% ethanol. We identified the food items and measured standard length of fishes in the pellets. After drying the food items on paper towels, we weighed them on a Sauter balance with 50 mg–200 g capacity.

Density of prey was determined from samples taken with a 1-m^2 throw trap (Kushlan 1981) at trapping stations located in different habitats (Fig. 1). A total of 99 samples were taken in marine habitats at two stations, 50 at a coastal lagoon (site 1; 10 on February 1, 10 on March 3, 10 on April 3, 10 on May 5 and 10 on June 22), and 49 at Ascension bay on the coast of Cedro Key (site 2; 10 on January 30, 10 on March 2, 10 on May 4, 9 on June 22). We present combined data for these two stations. In coastal saltwater mangrove swamps, we took 33 samples (site 3; 5 on February 17, 10 on March 21, 3 on April 26, 10 on May 28, 5 on June 28). In sawgrass marshes we took 41 samples at two stations, 15 in a marsh near Chunyaxché lagoon (site 4; 5 on February 18, 5 on March 14, 5 on June 23), and 26 in another inland marsh (site 5; 5 on February 17, 10 on March 21; 6 on May 28; 5 on June 28). Both places were dry in April, we present the combined data from these two stations. In inland freshwater mangrove swamps, we took 25 samples (site 6; 10 on March 26, 5 on April 28, 10 on May 29). In Chunyaxché lagoon (site 7) we took only 10 samples in December. As a measure of the prey density during the breeding season, we present the mean number of fishes per throw trap for each habitat.

Following Feisinger et al. (1981), we consider niche breadth as the degree of similarity

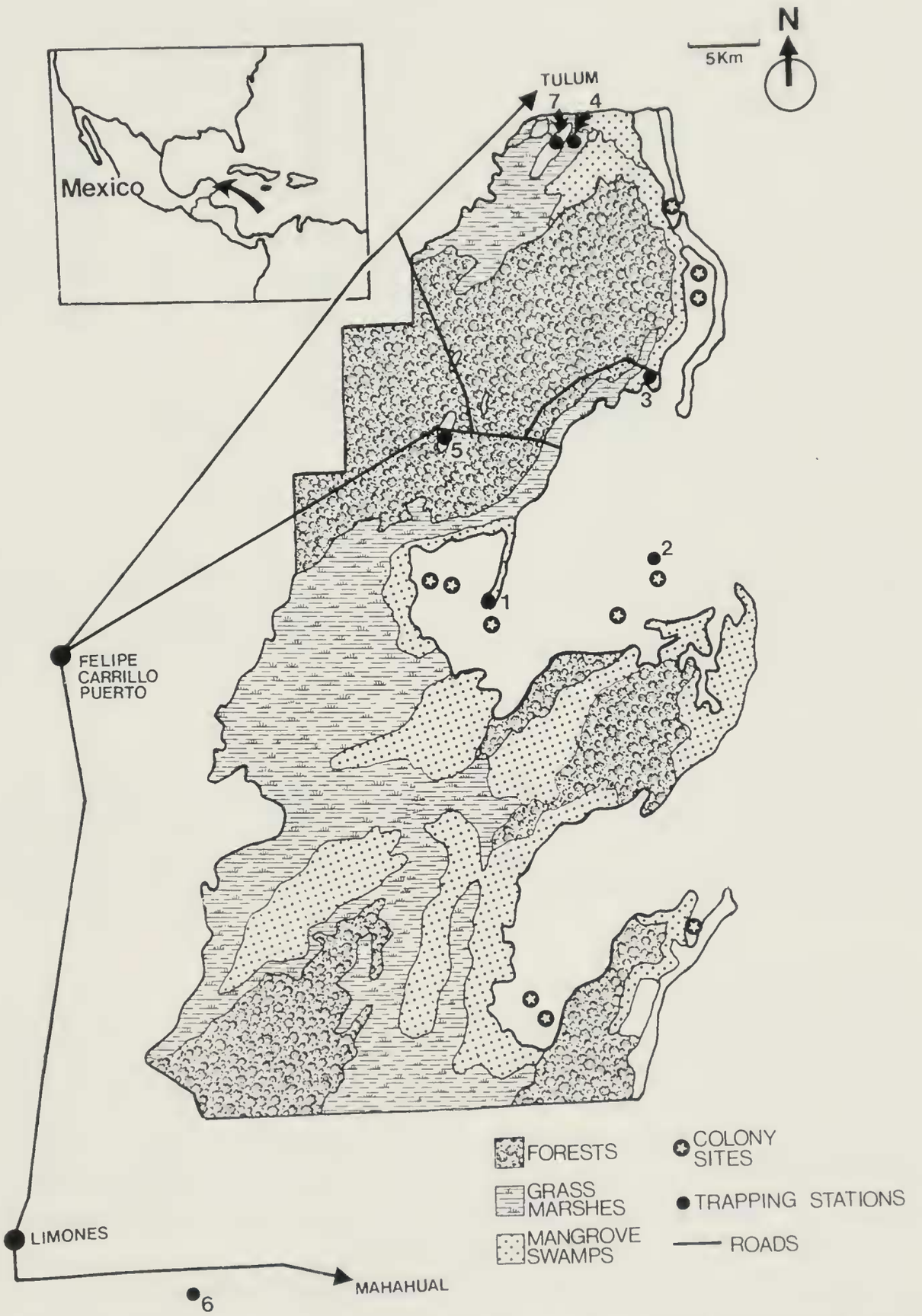

FIG. 1. Map of the Sian Ka'an Biosphere Reserve (Mexico) with vegetation types, colony locations and trapping stations.

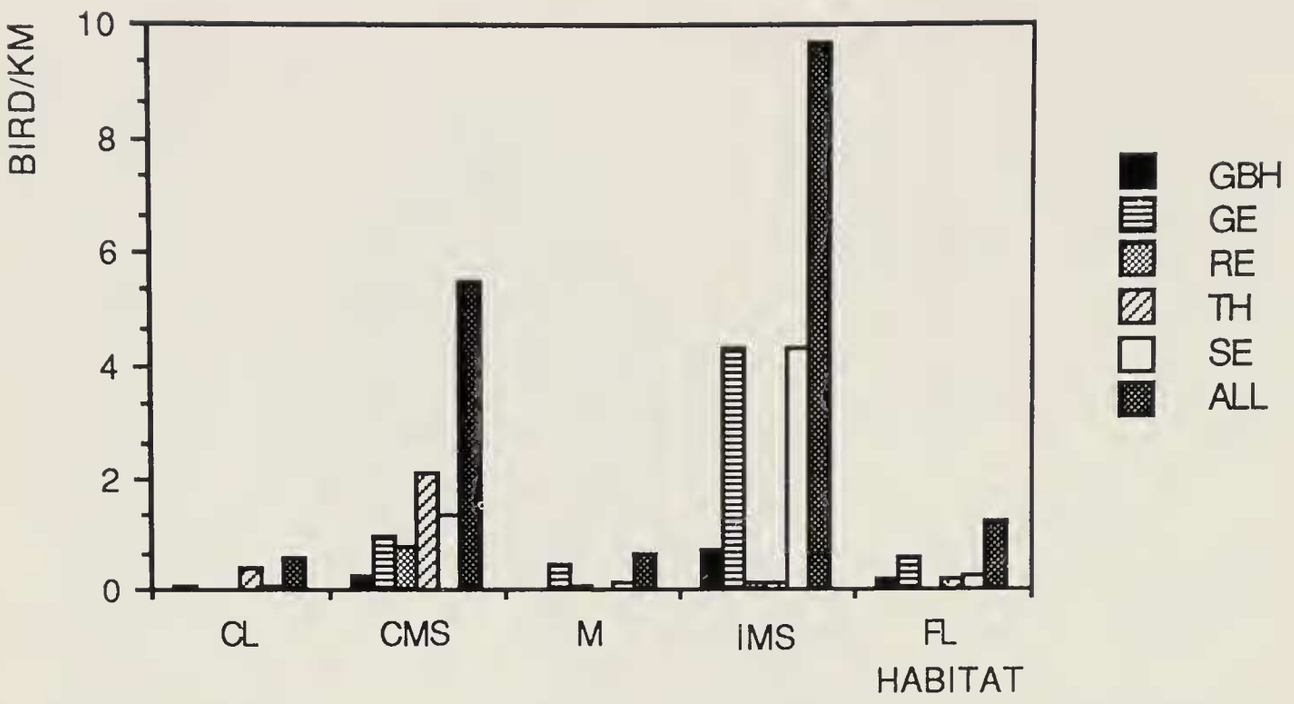

FIG. 2. Mean number of wading birds per kilometer on censuses conducted at different habitats during breeding period in Sian Ka'an Biosphere Reserve. CL = Coastal lagoon; CMS = Coastal mangrove swamp; M = Sawgrass marsh; IMS = Inland mangrove swamp. GBH = Great Blue Heron; GE = Great Egret; RE = Reddish Egret; TH = Tricolored Heron; SE = Snowy Egret.

between the frequency distribution of resources used by a species and the frequency distribution of resources available to them. We used the Proportional Similarity Index (Hurlbert, 1978, Feisinger et al. 1981), to compare niche breadth with regard to diet. Resource use similarity between species was measured with Horn's (1966) modification of Morisita's index. Dendrograms were built (average method) using the overlap indexes between species.

RESULTS

Transect counts showed that mangrove swamp was the most heavily utilized habitat (Fig. 2). We have no data for Boat-billed Heron, because this species is strictly nocturnal and censuses were conducted during the daytime. Reddish Egret and Tricolored Heron were closely linked to coast, while Great Blue Heron, Great Egret, and Snowy Egret were linked to inland. Consequently there is a high similarity in the use of habitat among species within each group (PS between pairs: GBH-GE = 0.93; GBH-SE = 0.87; GE-SE = 0.98; RE-TH = 0.85) (Fig. 3).

At Sian Ka'an, we could analyze only 19 prey items regurgitated by the Great Blue Heron (Table 1). The most frequent and important prey were White Ibis (*Eudocimus albus*) chicks (we found 9 small nestlings that still had the egg-tooth); other prey were fishes. Although the goldspotted killifish (*Floridicthys carpio*) was the fish consumed most often, it accounted for only 11% of the biomass, while two larger fish, the mullet (*Mugil curema*) and the redfin needlefish (*Strongilura notata*) accounted for 45%

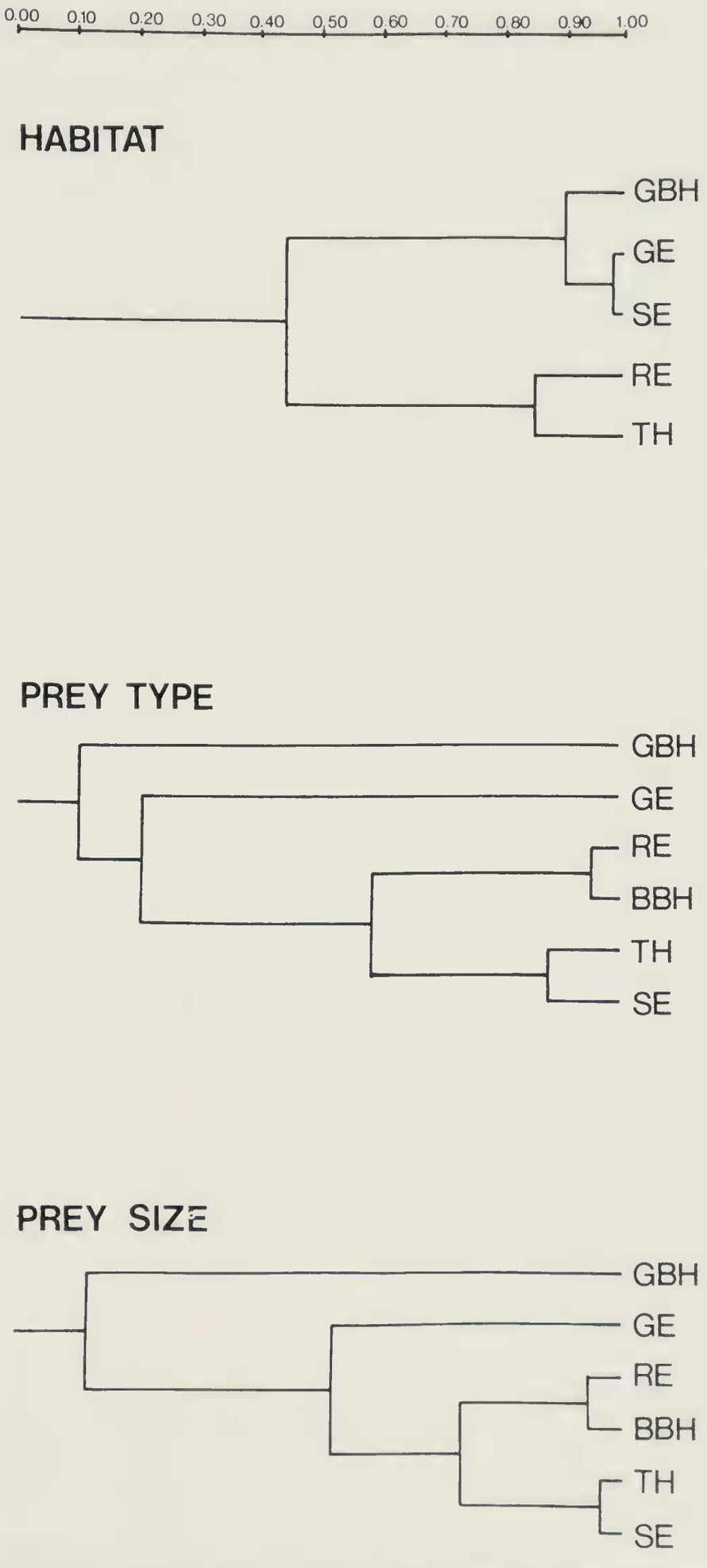

FIG. 3. Dendrograms (average method) based on the overlap indexes between species. GBH = Great Blue Heron; GE = Great Egret; RE = Reddish Egret; TH = Tricolored Heron; SE = Snowy Egret; BBH = Boat-billed Heron.

TABLE 1

PREY CONSUMED BY ARDEIDAE IN THE SIAN KA'AN BIOSPHERE RESERVE[a]

	Great Blue Heron		Great Egret		Reddish Egret		Tri-colored Heron		Snowy Egret		Boat-billed Heron	
	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B
Fishes												
Astyanax fasciatus	5	<1	63	48	—	—	6	13	14	19	—	—
Rhamdia guatemalensis	—	—	1	9	—	—	—	—	1	7	—	—
Cyprinodon variegatus	—	—	5	<1	69	37	23	16	27	9	57	28
Floridichthys carpio	37	11	1	4	7	44	7	18	—	—	23	63
Garmanella pulchra	—	—	2	<1	9	4	23	9	9	4	14	4
Belonesox belizanus	—	—	4	11	—	—	<1	3	—	—	—	—
Gambusia yucatana	—	—	9	1	13	3	6	4	11	6	3	1
Heterandria bimaculata	—	—	—	—	—	—	1	<1	—	—	—	—
Poecilia orri	—	—	4	6	—	—	25	34	24	27	—	—
Xiphophorus maculatus	—	—	—	—	—	—	1	<1	1	<1	—	—
Mugil curema	5	27	—	—	—	—	—	—	—	—	—	—
Eucinostomus argenteus	—	—	1	3	—	—	—	—	—	—	—	—
Eucinostomus gula	—	—	—	—	<1	1	—	—	—	—	—	—
Cichlasoma friedrichsthali	—	—	<1	1	—	—	—	—	<1	3	—	—
Cichlasoma urophthalmus	—	—	1	1	—	—	—	—	<1	1	—	—
Cichlasoma meeki	—	—	5	6	—	—	<1	<1	3	4	—	—
Cichlasoma octofasciatum	—	—	—	—	—	—	—	—	<1	<1	—	—
Cichlasoma salvini	—	—	<1	<1	—	—	<1	1	<1	4	—	—
Cichlasoma sp.	—	—	2	2	—	—	—	—	—	—	—	—
Petenia splendida	—	—	<1	2	—	—	—	—	3	15	—	—
Lophiogobius cyprinoides	—	—	—	—	—	—	—	—	—	—	—	—
Strongilura notata	5	18	—	—	<1	8	—	—	—	—	1	4
Atherinomorus stipes	—	—	<1	<1	<1	2	—	—	—	—	—	—

TABLE 1
CONTINUED

	Great Blue Heron		Great Egret		Reddish Egret		Tri-colored Heron		Snowy Egret		Boat-billed Heron	
	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B
Others												
Diptera	—	—	—	—	—	—	<1	<1	—	—	—	
Hemiptera	—	—	—	—	—	—	<1	<1	—	—	—	—
Isopoda	—	—	—	—	—	—	1	<1	—	—	—	—
Odonata	—	—	—	—	—	—	7	<1	—	—	—	—
Decapoda (prawns)	—	—	1	<1	<1	—	—	—	5	<1	—	—
Aves (*Eudocimus albus*)	47	43	—	—	—	—	—	—	—	—	—	—
Total	19	444	471	798	472	170	266	144	263	240	151	73

[a] Numbers are the percentage of items consumed (%N) and percentage of biomass consumed (%B) for each prey.

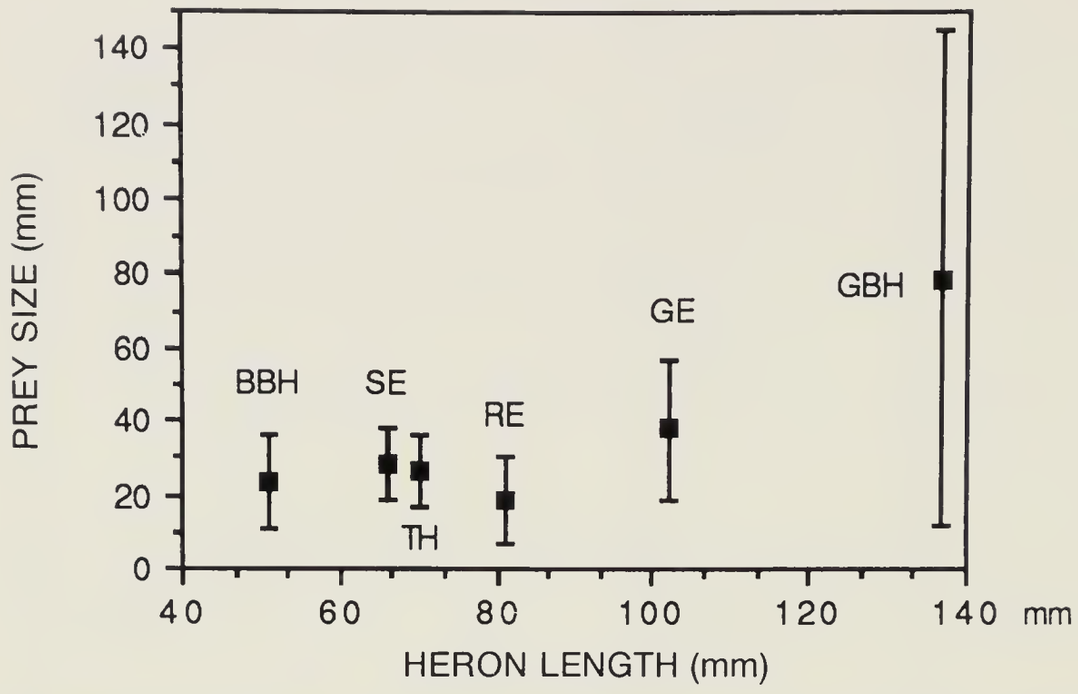

FIG. 4. Mean prey size taken by herons. Lines denote standard deviation. Heron length data taken from Blake (1977). GBH = Great Blue Heron; GE = Great Egret; RE = Reddish Egret; TH = Tricolored Heron; SE = Snowy Egret; BBH = Boat-billed Heron.

of the total biomass. The average prey size was 78.5 mm (Fig. 4), 89% of them between 30–80 mm.

Almost all Great Egret prey analyzed from Sian Ka'an were fishes, including 15 species, although prawns appeared in small numbers as well (Table 1). By far the most frequently consumed fish were characin (*Astyanax fasciatus*), 63% of total prey items and 48% of total biomass. Average size of prey was 38.9 mm (Fig. 4), 84% between 10–50 mm.

Most prey items of the Reddish Egret are fish, sheephead minnow (*C. variegatus*) which together with the goldspotted killifish represented 81% of total biomass. Reddish Egrets consume small prey, average size was 18.7 mm (Fig. 4), 92% between 10–30 mm.

At Sian Ka'an, invertebrates represented 8% of prey consumed by the Tricolored Heron, other being fishes of which five species accounted for 82% of prey items and 89% of the biomass (Table 1). Average size of prey was 26.2 mm, 92% between 10–40 mm.

Diet of the Snowy Egret at Sian Ka'an is comprised of 5% prawns and 95% fishes (Table 1). Five species of fishes accounted for 65% of the biomass. Average prey size was 26.2 mm, 90% between 10–40 mm.

All prey of the Boat-billed Heron examined at Sian Ka'an were fishes of five species; sheephead minnow and the goldspotted killifish the most frequent, accounting for 91% of total biomass (Table 1). Average size of fish was 23.3 mm, 95% between 10–30 mm.

Overlap indices among species, show great diet similarity between Reddish Egret-Boat-billed Heron and Tricolored Heron-Snowy Egret, both in prey type (RE-BBH = 0.95; TH-SE = 0.88) and prey size (RE-BBH = 0.94; TH-SE = 0.96; TH-BBH = 0.89; SE-BBH = 0.79) (Fig. 3).

Although we found a significant correlation ($r^2 = 0.80$) between size of heron and mean size of fish consumed (Fig. 4), it depends on the two large species for significance. Without these two species the correlation is nonsignificant ($r^2 = 0.15$), since there is no difference in prey size among the four other heron species.

Aquatic food resources available to wading birds differed among habitats (Table 2). In coastal lagoons, bays, and freshwater lagoons, the goldspotted killifish were the most common prey, in coastal mangrove swamps, the sheephead minnow and in inland mangrove swamps, characins (*A. fasciatus*), killifishes (*G. pulchra*) and livebearers (*P. orri*).

We found that the Reddish Egret has the broadest niche breadth, consuming prey almost in the same proportion to their availability in coastal mangrove swamps (Table 3), although some prey eaten by this species (*E. gula, S. notata, A. stipes,* and prawns) were not found in this habitat but in coastal lagoons or bays. We have no data for habitat use by the Boat-billed Heron, but the frequency distribution of prey is similar to that available in coastal mangrove swamps. Great Egrets and Snowy Egrets use mainly inland mangrove swamps; the PS values are intermediate, indicating they have some degree of specialization in their diets. In the case of the Great Egret, four prey species (*F. carpio, E. argenteus, A. stipes* and prawns) can be taken in coastal lagoons, and in the case of Snowy Egrets, prawns. Tricolored Herons, using mainly coastal mangrove swamps, show the lowest value of PS index. Nevertheless most prey taken by this heron are freshwater fishes commonly found in inland mangrove swamps (Table 2). The Great Blue Heron was excluded from the analysis because of the small number of prey samples (19 prey items).

Coastal mangrove swamps provide almost all prey to Reddish Egret, mangrove swamps (coastal and inland) to Great Egret, Snowy Egret and Tricolored Heron, and mangrove swamps, coastal and freshwater lagoons, to Boat-billed Heron.

DISCUSSION

Feeding habitat selection could be considered as the first step in resource partitioning, although the literature reveals considerable overlap among herons. For example, in coastal New Jersey, where five species of herons coexist, Great Blue Heron overlapped little with other species, but Great Egret showed no habitat segregation from Snowy Egret and very little from Tricolored Heron (Willard 1977). In an estuarine system of North

TABLE 2

MEAN NUMBER OF PREY PER THROW TRAP IN FIVE HABITATS OF THE SIAN KA'AN BIOSPHERE RESERVE DURING BREEDING PERIOD

Species	CL	CMS	M	IMS	FL
Astyanax fasciatus	—	—	0.10 (0.20)	2.32 (3.00)	—
Cyprinodon variegatus	0.07 (0.10)[a]	146.23 (279.21)	—	0.05 (0.10)	—
Floridichthys carpio	4.05 (1.29)	0.04 (0.09)	—	—	5.7
Garmanella pulchra	—	13.21 (27.63)	2.55 (3.08)	1.67 (3.03)	—
Gambusia yucatana	—	16.32 (35.71)	1.22 (1.62)	0.52 (0.57)	—
Poecilia orri	—	—	1.10 (1.94)	0.75 (1.25)	—
Eucinostomus argenteus	0.02 (0.03)	—	—	—	—
Cichlasoma urophthalmus	—	—	—	0.47 (0.82)	—
Cichlasoma meeki	—	—	—	0.50 (1.00)	—
Cichlasoma salvini	—	—	—	0.40 (0.80)	—
Cichlasoma octofasciatum	—	—	—	0.32 (0.65)	—
Gobionellus lyricus	0.05 (0.05)	—	—	—	—
Strongilura notata	0.04 (0.06)	—	—	—	—
Opsanus beta	0.03 (0.07)	—	—	—	—
Atherinomorus stipes	0.09 (0.20)	—	—	—	—
Prawns	0.96 (0.92)	—	—	—	—
Number of samples	99	33	41	25	10

[a] Standard deviations are in parentheses. LC = coastal lagoon; CMS = coastal mangrove swamp; M = grassmarsh; IMS = inland mangrove swamp; FL = freshwater lagoon.

TABLE 3
VALUES OF PROPORTIONAL SIMILARITY INDEX AMONG AVAILABLE AQUATIC FOOD RESOURCES OF FIVE HABITATS AND DIET OF THE SIAN KA'AN ARDEIDAE

Species	CL[a]	CMS	M	IMS	FL
Great Egret	0.03	0.16	0.17	0.53	0.01
Snowy Egret	0.06	0.44	0.44	0.45	0.00
Reddish Egret	0.08	0.86	0.23	0.18	0.07
Tricolored Heron	0.08	0.40	0.56	0.49	0.07
Boat-billed Heron	0.25	0.71	0.17	0.18	0.23

[a] CL = Coastal lagoon; CMS = coastal mangrove swamp; M = sawgrass marsh; IMS = inland mangrove swamp; FL = freshwater lagoon.

Carolina, Great Egrets, Tricolored Herons, and Snowy Egrets used mainly saltmarsh habitats; Tricolored Herons never used freshwater sites and used habitats similar to those used by Snowy Egrets (Custer and Osborn 1978). In Florida, Kent (1986) found no differences in habitat use among Snowy Egrets and Tricolored Herons in a marine habitat. In South Carolina, the Tricolored Heron and Snowy Egret both fed mainly in saltwater sites (Post 1990).

Nevertheless, at Sian Ka'an the availability of different habitat types, which vary from salt to freshwater, and from open to forested wetlands, allows the herons to segregate via the selection of different foraging habitats in two groups, Great Blue Heron-Great Egret-Snowy Egret that used mainly freshwater habitats and Reddish Egret-Tricolored Heron that used marine habitats. Freshwater mangrove swamps at Sian Ka'an are important habitat for herons as they retain water during most of the dry season.

Within a habitat, the second step towards resource partitioning is food selection. At Sian Ka'an, among the first group of species considered, prey type taken by Great Blue Heron, Great Egret, and Snowy Egret differed considerably.

Although Tricolored Heron used mainly coastal mangrove swamps and Snowy Egret inland mangrove swamps, the two species ate similar prey. Samples taken in these two habitats show different prey composition, but we took these samples in extreme situations of salinity. Prey probably were distributed in a continuum, changing gradually between extremes, allowing herons to take similar prey at different sites, Tricolored Heron near the coast and Snowy Egret inland. In other places, these two herons also have a great similarity in their diets. Using data provided by Jenni (1969) from Lake Alice, Florida, we calculated an overlap index of 0.86 between the two species (0.88 at Sian Ka'an), and in a marine habitat also in Florida, Kent (1986) found overlap of 0.80.

We found no differences in the other two species, Boat-billed Heron and Reddish Egret, that eat almost the same prey, but the different patterns of activity, the first being strictly nocturnal and the second diurnal, obviously segregate these species. Nevertheless the bulk of their diets is composed of *C. variegatus* that is by far the most abundant prey species (Table 2).

In some cases, it has been considered that capture of different prey lengths is the most important factor in resource partitioning, with the body length of the prey positively related to the body size of the heron (Whitfield and Blaber 1978, Hom 1983). In our case, there is a correlation between size of heron and size of prey, but prey size was not important in heron segregation, since four species, Boat-billed Heron, Reddish Egret, Tricolored Heron, and Snowy Egret prey on similar sizes. As has been discussed by Niethamer and Kaiser (1983), body size and prey size are probably correlated between sets of large and small herons rather than along a continuum.

Feeding behavior is another mechanism considered important in resource partitioning. At Sian Ka'an the pairs, Tricolored Heron-Snowy Egret, and Boat-billed Heron-Reddish Egret, that exhibit different feeding behavior in other locations (Meyerriecks 1962, Mock 1975, Kushlan 1978, Biderman and Dickerman 1978, Willard 1977, Rodgers 1983, Kent 1986) took similar types of food. Kent (1986) suggests that behavioral differences alone should not be considered to be a partitioning mechanism, and our results confirm this suggestion.

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